FLIGHT AND SWIMMING REFLEXES IN GIANT WATER BUGS

HUGH DINGLE

Department of Zoology, University of Michigan, Ann Arbor, Michigan

Loss of substrate contact or tactile stimulation initiates a "classic" flight reflex in insects (Fraenkel, 1932; Chadwick, 1953). Either one or both factors can operate to elicit the reflex; flight ceases when the legs again make contact with the substrate. When giant water bugs were removed from substrate contact, they did not fly, but instead swam. If they stopped, they would begin again with direct tactile stimulation. In short, they appeared to swim in those situations in which terrestrial insects fly. Although a few of the water bugs eventually flew, they did so only after a considerable period; during this time they were swimming. This study is an attempt to analyze the swimming and flight reflexes of these giant water bugs.

MATERIALS AND METHODS

Two species of giant water bug were used, *Lethocerus americanus* and *Benacus griseus*. The bugs were captured by light trap (a sheet and a Mercury Vapor bulb, General Electric H100 L4) between April and September, 1960, on the Edwin S. George Reserve, the wildlife reserve of the University of Michigan, Livingston County, Michigan. A total of 60 animals were used; they were kept in the laboratory on a diet of small fish.

Giant water bugs are large (about 4.5 to 6.5 cm. long) dorso-ventrally flattened predaceous insects. The forelegs are raptorial with enlarged femora and bear only a single tarsal claw; the middle and hind legs are adapted for swimming; they are flattened and bear hairs so arranged as to be raised during the power stroke of the leg and depressed during the forward stroke. The swimming legs have the usual two tarsal claws. Respiration is accomplished with two retractable tubes which protrude from the posterior end of the abdomen (Fig. 4).

In the analysis of swimming and flight reflexes, the bugs were suspended from an applicator stick using a mixture of paraffin, beeswax, and resin to attach the stick to the prothorax. They were then placed in the air stream of a wind tunnel and given a stick to hold which served as a contact stimulus for the legs. The wind tunnel was made from wood and light cardboard and included a cardboard honeycomb baffle to cut down turbulence which, as determined by smoke, was slight; the diameter of the tunnel mouth was 10 cm. For wind a fan was used, the speed of which could be controlled by a rheostat. Wind speed was calibrated with a Taylor Briam's Type Anemometer (No. 3132); it ranged up to 7.0 m./sec. In certain experiments small jets of water or air, which were directed by attaching a glass tube to a rubber hose, were used; no attempt was made to measure the velocity of these.

Swimming

Loss of substrate contact almost invariably elicited swimming movements.   The rate and duration of these movements varied.   The initial rate for 19 bugs in quiet air ranged from 120 to 320 strokes per minute with an average of 206; the duration ranged from 6 seconds to more than 180 seconds with an average of 51 seconds. This swimming response was clearly distinguishable from haphazard movement; the forelegs were carried forward of the head, and in intense swimming they were stretched forward almost full length.   The abdomen was raised, and the middle and hind pairs of legs were usually protracted and retracted (see Hughes, 1952, for definitions) simultaneously and not alternately as reported by Lauck (1959) for a different species.   Although alternation was never observed, it was noted that the two pairs were sometimes not quite simultaneous.   The two legs of each pair operated simultaneously as reported by Lauck.

Swimming could be stopped by giving the bug a stick to hold.   Contact with any one tarsus was sufficient; when the bug made contact, the ipselateral leg reached for and grasped the stick.   Swimming also ceased with contact on other parts of the leg, *e.g.* tibia and femur, especially if tension was applied; Diakonoff (1936) reports similar results in a flying cockroach.   Sometimes, however, the bug dropped the stick or "walked" off it and continued to swim.   If the stick was removed carefully, leaving the legs folded under the body, the bug usually remained motionless. Swimming in such a situation could be initiated by gently lowering the legs until they were outstretched.   Bugs also stopped swimming on occasion when they presumably saw the stick in front of them, reaching out and seizing it with the forelegs.   Touching any part of the forelegs resulted in attempts to grasp the stick.

In experiments testing the effect of increasing wind velocity, the bugs were holding a stick which was removed at each higher velocity; it was returned when the bug stopped swimming.   After 30 seconds the velocity was increased by about 1 m./sec. and the process repeated.   Rate and duration of swimming increased up to a point and then decreased; this decrease will be discussed in greater detail below. The lowest wind velocity measured, 0.5 m./sec., was sufficient to increase rate and duration in 50% of the bugs; for the remainder higher velocities were needed. Twenty per cent of the bugs reached their maximum rate at 1.6 m./sec.; maxima were attained up to 6.7 m./sec.   Maximum durations occurred from 0.5 to 7.0 m./sec., the total range used in these experiments.   Except for one bug which gave a brief burst of strokes at around 400/minute, the greatest rate of swimming observed was 320 strokes/minute which was reached by half the animals; they could not be induced to swim faster.   If wind was blown on an animal from the side, it often responded with compensatory movements of the legs on the opposite side. Figure 1 shows rate and duration with increasing wind speed for three representative bugs.

If the bug was holding an object, wind alone initiated swimming and consequent dropping of the stick in 25% of the cases.   Usually, however, swimming occurred only when wind was combined with loss of substrate contact.   Ordinarily loss of contact was the significant stimulus, but often the few bugs that would not swim with just loss of contact could be induced to do so if wind was simultaneously applied.   A bug that had been swimming, but had stopped, would start again when wind was applied.

In addition to loss of contact and wind, direct tactile stimulation, *e.g.* of the abdomen, and vibration or movement of the bug while suspended also caused swimming. Any movement, whether up and down or to and fro, and any vibration, caused either by tapping the stick to which the bug was attached or pounding the
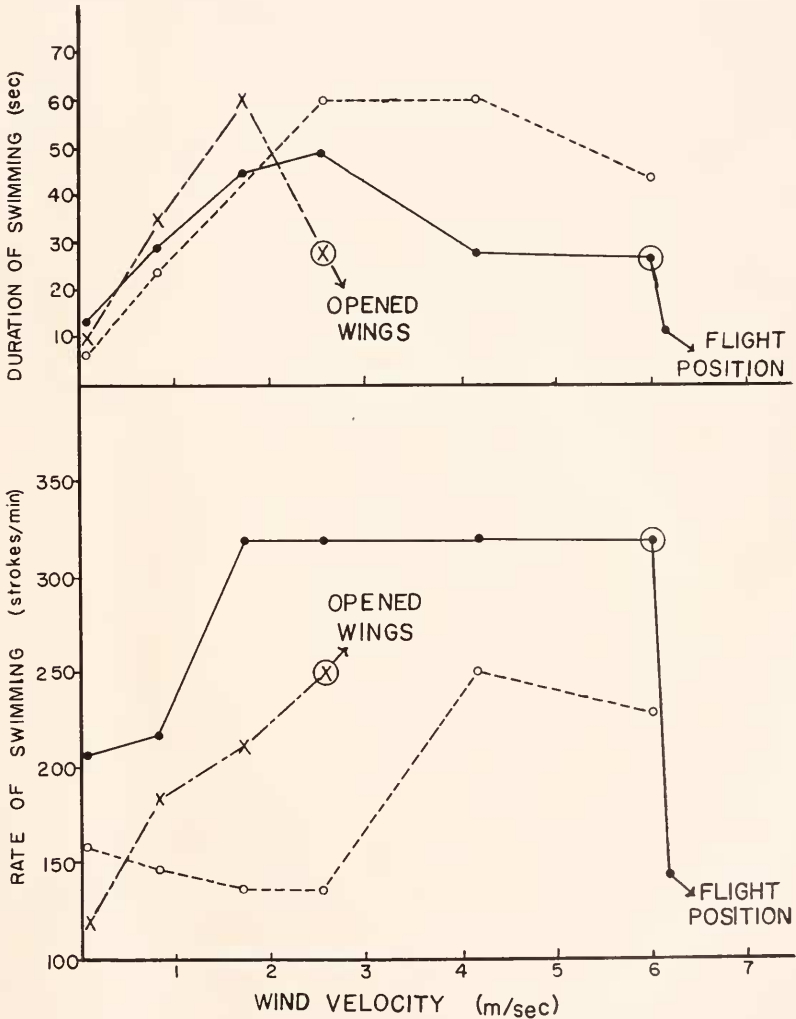

FIGURE 1. Graphs of rate and duration of swimming plotted against wind velocity for three representative bugs. Circled points indicate beginning of first noticeable flight preparation movements; these were not observed in one animal.

table with the fist, elicited the swimming. Fraenkel (1932) reports that flight in *Vespa, Calliphora, Apis, Schistocerca,* etc. resulted from a blow on the abdomen, and Diakonoff (1936) found that cockroaches flew if allowed to fall, a phenomenon he termed a "fall reflex."

Not too surprisingly, suspended bugs also swim when placed in water, although the swimming is very quickly adapting, lasting only a few seconds. Swimming can be further induced by directing a current at the bug, moving the animal through the water, or by taking the animal out of the water, but again the swimming is quickly adapting. By far the most rapid swimming comes when the bug is allowed to touch some object with its forelegs which it then attempts to grasp. This too adapts, but after a longer time. Swimming also follows on occasion when the bug presumably sees an object in front of it. A water jet directed at the bug from one side causes some compensatory movements of the legs on the opposite side. The same results are observed when the bug is rotated through the water in a small circle; this phenomenon was also recorded by Hughes (1958) in *Dytiscus*.

Sense organs mediating swimming

Fraenkel (1932) found that his insects would not stop flying when their tarsi were removed, which led him to believe that a receptor sensitive to contact was located there. Diakonoff (1936), however, was unable to find sensilla on the tarsal claws of the cockroach and found that in addition to the tarsi, stimuli on the tibiae, femora, and even coxae could stop flight. Since water bugs swam on loss of substrate contact, presumably a mechanism similar to that eliciting flight in the above cases is involved. It was found that swimming ceased either with tarsal contact or with stimuli on the tibiae or femora.

Touch receptors seem to be implicated in the instance of more rapid swimming when the bug touches an object with its forelegs. The leading edges of the femora of these bugs are covered with an extensive sensory area, and this area when touched is especially apt to elicit increased swimming. The exact nature of these receptors and others at the same spot affords a promising line of future investigation.

Specific receptors, eliciting swimming in response to either air or water currents, have not been located. With the forehead, eyes, hair beds behind the eyes, hair beds at the bases of the fore femora, and hair beds at the junction of the pro- and mesothorax covered individually or all together with paraffin, the swim reflex did not appear to be hindered in any way. Although the antennae were not removed completely, located as they are in grooves under the eyes, the bugs still began to swim in currents after an operation to destroy the brain, indicating that neither the antennae nor for that matter any other head receptors innervated by the brain are mandatory for the initiation of this swimming. It is suspected that swimming in response to current can be initiated by any of several receptors located on the body. Certainly the body possesses many groups of hairs located at various joints and articulations, and that several of them may be "current receptors" is indicated by the fact that a bug will swim in a current coming from virtually any direction.

When the bugs are in water, however, there do seem to be specific sense organs which initiate swimming. The first hint of such receptors came while a bug whose nervous connectives had been severed between the pro- and mesothoracic ganglia, the cut being made just posterior to the forelegs, was being studied. Such an insect loses all muscle tone posterior to the cut, and the legs hang limply. When this bug was put in water, the legs began to protract and retract slowly and rhythmically with enough force to give the bug some forward momentum. Further observation revealed that this swimming commenced only when the legs had floated

up so as to be extended almost laterally from the body. Swimming was also observed when the bug was held upside down and the legs were in almost the same position as when floating, but this was never more than a few strokes.

In attempts to locate more closely the receptors responsible for this swimming response, the leg segments and joints from all four swimming legs were removed successively with the following results:

(1) Removal of first tarsal segment and joint between the two tarsal segments —bug swam, but kept legs rather sharply bent at tibio-femoral joint.

(2) Removal of second tarsal segment and tibio-tarsal joint—bug swam with shorter and more rapid strokes.

(3) Removal of tibia and tibio-femoral joint—bug swam with short, rapid, and choppy strokes that were not well co-ordinated.

These results seemed to indicate that the receptors responsible for the swimming response were located somewhere proximal to the tibia. Because of the flotation of the legs which seemed to be necessary, the location was suspected to be at either the coxo-trochanteral or femoro-trochanteral joint; the former location appeared to be the more likely. Hair beds are located on the trochanters at this joint just distal to the trochanteral condyles (Fig. 2). When the legs hung down as they did when the bug was suspended, these hair beds were covered by membranous cuticular folds present on the coxae; when the legs floated in water, the hair beds were uncovered.

In bugs with the connectives severed between the pro- and mesothoracic ganglia, the trochanteral hair beds on various legs were burned with a hot needle. If these were destroyed on all four swimming legs, the bugs showed no response when placed in water; if the hair beds on the middle legs were destroyed, the hind legs still swam, with the converse true if the hind leg hair beds were burned. In a bug lacking the hair bed on one middle leg, the other three legs swam in the usual fashion while the operated leg gave strokes on each alternate stroke of the rest; with the hair beds on three legs burned, only the single intact (hind) leg gave swimming strokes, and these were slower than previously. In bugs with the central nervous system intact, when the hair beds were destroyed on all four swimming legs, walking was more or less as usual, but the bugs seemed to have difficulty gaining traction on surfaces where normal animals had no difficulty. In both water and air, swimming strokes were short and jerky; in air, swimming proved also to be more difficult to induce than in normal individuals. These hair beds thus appear to be intimately involved with swimming and co-ordination of leg movements.

The trochanteral hair beds are apparently excited by the cuticular folds which cover them when the legs hang down or are folded beneath the body. As the legs float up when the bug is in water, these folds roll back progressively until the hair beds are uncovered when the legs are extended laterally. Presumably, then, when stimulation of the hair bed by the cuticular fold ceases, the leg begins to swim. Possibly direct contact with water prompts the swimming movements to some extent although this is not the only factor since inverted bugs with severed connectives also swim. Pringle (1938) described three hair plates on the leg of the cockroach, including one at the coxo-trochanteral joint, which he believed were also stimulated by a cuticular fold; the hair plates were incompletely adapting.

Because of the location and action of these sense organs, Pringle considered them "position" receptors. The action of the hair beds on the legs of the giant water bug seem to have an analogous function, *i.e.* registering the position of the legs until they finally reach swimming position, whereupon the swimming reflex is triggered.

This proposed action of the hair beds helps to explain some aspects of the bugs' behavior. As mentioned earlier, a suspended bug tends not to swim when its legs are folded under the body as when grasping a stick. This lack of response would, on the above explanation, be due to the covering of the hair beds by the cuticular folds. In nature the bugs cling to submerged vegetation; if they were torn free, the resultant flotation of the legs would provoke swimming and lead to regaining of foothold.
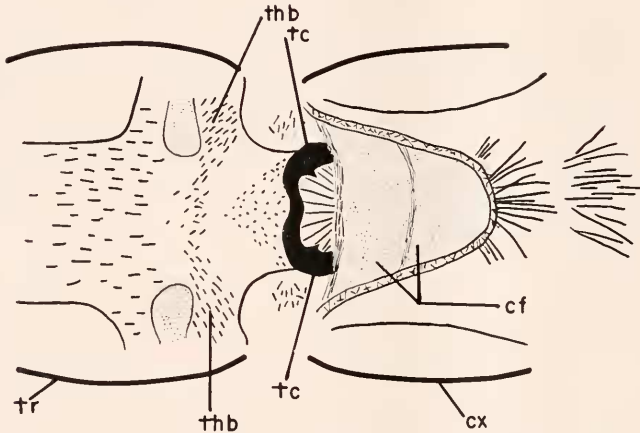

FIGURE 2. Ventral view of the coxo-trochanteral joint. The coxa and trochanter have been depressed dorsally as they would be if the leg were floating to expose the trochanteral condyles and hair beds. When the leg hangs down, the cuticular fold covers these two structures; the fold rolls back as the leg floats up. tr, trochanter; cx, coxa; thb, trochanteral hair bed; tc, trochanteral condyles; cf, cuticular fold.

Vision also seems to affect swimming. If a suspended bug is rotated through the water in a tight circle, the inside legs show compensatory movements that oppose the direction of rotation. In a bug with its eyes covered, the compensatory movements are so reduced as to be almost negligible. Hughes (1958) found reduction in the compensatory movements of a rotated *Dytiscus* when the eyes were covered.

FLIGHT

Pre-flight behavior in giant water bugs follows a fairly elaborate and somewhat varied pattern. The first sign is usually scraping of the hind legs over the wings and depression of the abdomen. There then follows twitching of the legs, which in the more advanced stages can be quite violent; this twitching is often accompanied by "shrugging" movements in which the pterothorax and abdomen are moved rapidly anterior-posterior at the articulation between the pro- and mesothorax. The wings can, at least from the author's observations, be opened at any stage of these preparations.

This rather extensive pre-flight behavior is apparently necessary because of a ball and socket mechanism which locks the wings to the pterothorax (Lauck, 1959) ; this mechanism is illustrated in Figure 3. The ball protrudes posteriorly from the dorsal margin of the mesepimeron and inserts into the socket on the costal margin of the hemelytron; the mesal border of the clavus matches the wing grooves on the postnotum. In order to open the wings, the bug must first release the ball and socket mechanism, which is probably accomplished, according to Lauck, by a combination of contractions of the third axillary muscle and the tergo-sternal
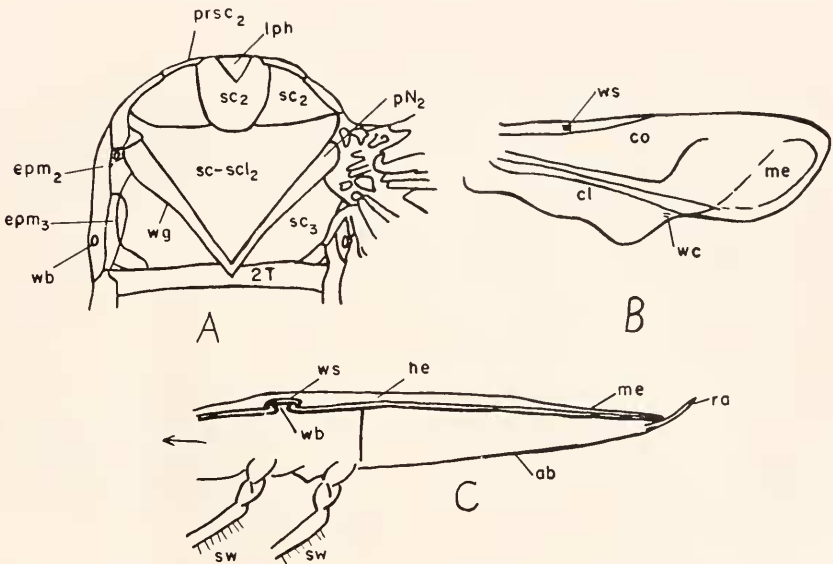

FIGURE 3. *Lethocerus:* views of pterothorax and hemelytron to show position of wing ball (wb) and wing socket (ws). The posterior margin of the clavus (cl) fits along the wing groove (wg). A: Pterothorax with wings on left side removed. prsc, prescutum; ph, phragma; sc, scutum; sc-scl, scuto-scutellum; pN, postnotum; epm, epimeron; wb, wing ball; wg, wing groove; T, tergite of abdomen. B: Ventral aspect of left hemelytron. ws, wing socket; co, corium; cl, clavus; me, membrane; wc, wing clip. C: Diagram showing wing locking mechanism. he, hemelytron; ra, respiratory apparatus; ab, abdomen; sw, swimming leg. Arrow points anteriorly. A and B redrawn from Lauck (1959) by permission of the publishers. Not drawn to same scale.

muscles which levate the wings. The various violent leg twitchings, depressions of the abdomen, and oscillations of the body characteristic of the pre-flight behavior are apparently the result of attempts by the animal to get the wings unlocked.

There is, however, another possible reason for the pre-flight movements. Krogh and Zeuthen (1941) note that lamellicorn beetles "pump" before flight; they measured the rise in temperature of the muscles during "pumping" and found that not until the temperature was at least 32° C. would the beetles fly. The flight temperature varied from 32° to 37°. Poor fliers like the beetles needed higher body temperatures to fly than did sphingid moths which are quite active fliers. Since giant water bugs are relatively poor fliers, it is possible that the pre-flight movements raise the body temperature enough to fly.

In spite of the extensive pre-flight behavior in most animals used, only a few actually flew; of 44 suspended bugs, four flew while four more opened their wings, but did not fly. Several others showed a tendency to assume the flight position, but never reached the stage of opening the wings. The flight position is shown in Figure 4. The swimming legs are carried folded flat against the underside of the body, although not in this illustration; the abdomen is depressed; and the respiratory apparatus is fully extended and held erect. Those bugs that did fly were, with one exception, suspended for five minutes or longer and most of the time in winds of greater than 6 m./sec. Weis-Fogh (1956) found that in locusts wind speeds of greater than 2 m./sec. were necessary to initiate flight.
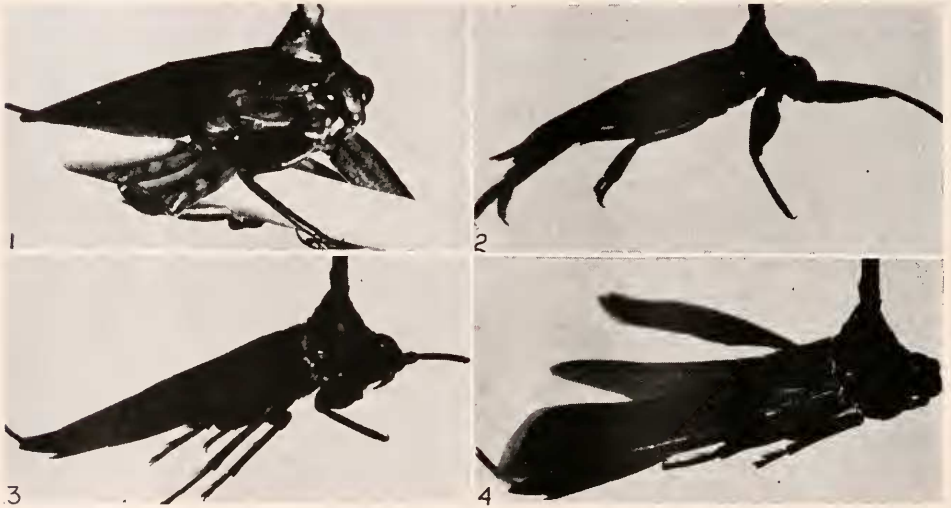

FIGURE 4. (1) Suspended bug holding drinking straw as substrate contact. (2) Swimming bug; swimming legs are approximately at the end of the backstroke. (3) Bug in flight position; note position of swimming legs and respiratory apparatus compared with (2). (4) Bug with wings open; again note position of swimming legs and respiratory apparatus.

Once a bug had flown, the threshold for further flight or wing opening was lowered considerably. Flight could be stopped by bringing the bug into contact with the substrate and could usually be initiated again if the animal was suspended. If flight was not induced by suspension, it could then be initiated by putting the bug into a wind. The contact-loss of contact mechanisms is presumably similar to those mentioned above when discussing swimming.

The stimulation of flight by wind is of some interest. It was found that a jet of compressed air delivered through a bit of glass tubing was most effective in promoting flight or wing opening (in bugs that had already flown or opened their wings) when it was aimed directly at the bugs' heads from in front. In these bugs the wings invariably opened while the air jet was blowing on the head and would close when it was removed. If the area of the head above the beak and between the eyes was covered with paraffin, the response disappeared; it reappeared when the paraffin was removed. This was true for all 8 of the bugs tested. Partial

covering of the forehead with paraffin did not abolish the response; so long as part of it was exposed, the response was maintained. Examination of a bug's head under the dissection microscope revealed that the area being considered was covered with fine hairs, virtually invisible to the naked eye, which are presumably responsible for the initiation of wing opening or flight when stimulated by air currents. Weis-Fogh (1956) found 5 paired groups of wind-sensitive hairs on the head of the locust which were sufficient for both the initiation and maintenance of flight, but were not necessary for either. Aside from the hair beds, flight in the locust could be initiated by loss of tarsal contact, which was also found to be true with giant water bugs, and could be maintained by wind on the moving wings, which was not observed in this study. In both bugs and locusts the direction of the wind impinging on the hair beds was not particularly important.

Interaction of Flight and Swimming

There seems to be little doubt that the initial response of these insects to loss of substrate contact is swimming. As previously mentioned, with increased wind speed both rate and duration of swimming increased up to a point, which varied from one bug to another, and then decreased. At first it was thought that this was due to fatigue or adaptation, but careful observation of the bugs' behavior revealed that the most likely possibility was the inhibition of swimming by the pre-flight activities even in those bugs, the most usual, in which neither flight nor wing opening ever occurred. In the latter cases, however, the bugs often did assume flight position with the legs, abdomen, and respiratory apparatus (Fig. 4). Reduction of swimming also occurred when the bugs were given successive bursts of wind at a constant speed (5.9 m./sec.), although it was not so marked.

The Central Nervous System

The anatomy of the giant water bug central nervous system reflects the general anatomy and habits of the bug. The sub-oesophageal and prothoracic ganglia are fused into one ganglion located between and slightly anterior to the bases of the coxae of the raptorial prothoracic legs which are innervated from this ganglion. The meso- and metathoracic ganglia are also fused into a common structure located between the bases of the mesothoracic legs. This ganglion innervates all four swimming legs and the wings. The brain and circumoesophageal connectives appear to be grossly similar to those of other insects.

A bug with its brain destroyed (using a hot needle) moved about apparently quite normally. Closer observation, however, revealed certain rather distinctive abnormalities. For instance, when walking about, a brainless bug tended to lose its balance and fall over on its back when stepping over small objects; once on its back it had considerable difficulty righting itself, often being unable to do so. An intact animal would, when placed on its back, bridge up with its forelegs and give a hard kick with the middle and hind legs on one side pivoting over on the tip of the abdomen; a brainless bug, on the other hand, was unable to bridge as high with the forelegs or to use the swimming legs effectively to flip over. When placed in wind, the brainless bugs differed from the normal in two ways. First, they would swim for much longer periods, usually showing no signs of slowing

down; and second, they accepted a stick and thus ceased swimming much more readily. Roeder (1937) and Roeder *et al.* (1960) note that the praying mantis also exhibits hyperactivity with the brain destroyed, walking until exhaustion. Bugs with only half the brain destroyed carried out the classic maneuver of circling to the intact side. Severing the connectives just behind the forelegs resulted in loss of tone in the swimming legs, but the legs continued to swim when the animal was placed in water, as noted above; the forelegs often twitched for a time after the cut was made.

Discussion

The fact that when the trochanteral hair bed on one mesothoracic leg was destroyed, that leg swam on the alternate strokes of its counterpart seems to indicate transfer of impulses from one side of the mesothoracic ganglion to the other. Rowe (1960) has shown electrically that such intraganglionic transfer occurs, while several authors (*e.g.* Diakonoff, 1936; Ten Cate, 1941; and Hughes, 1957) have behavioral evidence for it. Destroying the hair beds on both of a pair of swimming legs resulted in loss of activity of that pair while the other two continued to swim. Thus, as was the case with Pringle (1940), the author was unable to demonstrate transfer of a reflex from one thoracic ganglion to another even though the meso- and metathoracic ganglia are, in this case, fused.

Roeder (1937; see also Roeder, 1953) proposed a model for the operation of the insect central nervous system; in this model the brain exercises inhibitory control over locomotion, in view of the locomotor hyperactivity of brainless insects. Since giant water bugs are also hyperactive when brainless, they appear consistent with Roeder's model. Bugs whose connectives had been severed posterior to the fused sub-oesophageal and prothoracic ganglia lost all muscle tone in the swimming legs, but because of their fusion, it was not possible to separate the two ganglia functionally. There is some evidence from studies on cockroaches (Diakonoff, 1936; Ten Cate, 1941; Chadwick, 1953) that the prothoracic ganglion may be essential for normal co-ordination.

If Hemiptera are secondarily aquatic, then the swimming reflex of aquatic forms like the giant water bugs may be considered a modification of the flight reflex of exclusively terrestrial insects. The reflexes, under natural conditions, would be triggered by similar sets of circumstances. A floating water bug, for instance, is free of substrate contact, and a swimming reflex might result, particularly since the usual habit of the bug is to cling to floating vegetation. A falling terrestrial insect, on the other hand, is also free of substrate contact and generally flies. The two situations of floating and being air-borne are essentially the same, and the reflexes of a particular insect, be they swimming or flying, are modifications to suit the particular medium.

The escape responses are similarly modified. Strong tactile stimulation, especially of the abdomen (Fraenkel, 1932), causes terrestrial insects to leap off the substrate and fly. In the aquatic bugs tactile stimuli or vibrations result in violent swimming whether the animal is in water or suspended in air.

But if the swimming reflex is a modification of the flight reflex, why then do the water bugs sometimes fly? There appear to be two major possibilities. First, the body posterior to the articulation of the pro- and mesothorax of a bug

suspended in air hangs down at a rather sharp angle; in water this part of the body is buoyed up. Diakonoff (1936) reports that movement at the pro-meso-thoracic articulation of the cockroach results in a "fall reflex" that elicits flight and is apparently due to stimulation of the numerous receptors at the articulation. A similar mechanism may stimulate flight in giant water bugs. Second, when the bugs are suspended in wind, the hair beds on the head, which have been shown to be receptors concerned with flight, are stimulated. This stimulation, if strong enough or if summation occurred, would presumably overcome the swimming reflex and elicit flight.

One would predict, on the assumption that swimming with lack of substrate contact is a modification of a flight reflex, that it would be a fairly general adaptation among aquatic insects. This prediction appears to be largely true. Hughes (personal communication) has observed the swimming reflex in *Hydrophilus* and *Dytiscus*, and the author has found it in gyrinids, hydrophilids, dytiscids, corixids, and the genus *Belostoma*, as well as in the giant water bugs discussed here. Further investigations of the phenomenon in these groups are now in progress.

Summary

1. Giant water bugs swim when suspended free of the substrate. This situation contrasts with that of terrestrial insects which fly when freely suspended. Swimming can be stopped by returning contact to the bugs.

2. Suspended bugs respond to wind with a general increase in rate and duration of swimming, followed by a decrease in both.

3. When bugs are in water, swimming is stimulated by a hair bed located on the trochanter at the coxo-trochanteral joint. These hair beds seem to be stimulated by cuticular folds which cover them when the legs hang down, but roll back and leave them uncovered when the legs float, resulting in swimming.

4. Flight or wing opening occurred with 8 of 44 suspended bugs. A hair bed on the head functions in both the maintenance and initiation of flight in response to wind.

5. The bugs possess an elaborate pre-flight behavior which is apparently necessary to unlock a ball and socket mechanism attaching the wings to the pterothorax. This pre-flight behavior inhibits swimming and causes the decline in rate and duration mentioned in (2) above.

6. In the central nervous system the sub-oesophageal and prothoracic ganglia are fused, as are the meso- and methathoracic ganglia. There is behavioral evi-

dence for transmission of impulses across a ganglion, but not from one ganglion to another, even though the ganglia are fused.

7. There is evidence that the swimming reflex is a general phenomenon; apparently it is an aquatic modification of the flight reflex.

LITERATURE CITED

CHADWICK, L. E., 1953. The flight muscles and their control. *In*: Roeder, K. D., Insect Physiology. New York, Wiley. Pp. 648–655.

DIAKONOFF, A., 1936. Contributions to the knowledge of the fly reflexes and the static sense in *Periplaneta americana* L. *Arch. Néerl. Physiol.*, **21**: 104–129.

FRAENKEL, G., 1932. Untersuchungen über die Koordination von Reflexen und automatisch-nervösen Rhythmen bei Insekten. I. Die Flugreflexe der Insekten und ihre Koordination. *Zeitschr. vergleich. Physiol.*, **16**: 371–393.

HUGHES, G. M., 1952. The co-ordination of insect movements. I. The walking movements of insects. *J. Exp. Biol.*, **29**: 267–284.

HUGHES, G. M., 1957. The co-ordination of insect movements. II. The effect of limb amputation and the cutting of commissures in the cockroach (*Blatta orientalis*). *J. Exp. Biol.*, **34**: 306–333.

HUGHES, G. M., 1958. The co-ordination of insect movements. III. Swimming in *Dytiscus, Hydrophilus,* and a dragonfly nymph. *J. Exp. Biol.*, **35**: 567–583.

KROGH, AUGUST, AND ERIK ZEUTHEN, 1941. The mechanism of flight preparation in some insects. *J. Exp. Biol.*, **18**: 1–10.

LAUCK, DAVID R., 1959. The locomotion of *Lethocerus* (Hemiptera, Belostomatidae). *Ent. Soc. Amer. Annals*, **52**: 93–99.

PRINGLE, J. W. S., 1938. Proprioception in insects. III. The function of the hair sensilla at the joints. *J. Exp. Biol.*, **15**: 467–473.

PRINGLE, J. W. S., 1940. The reflex mechanism of the insect leg. *J. Exp. Biol.*, **17**: 8–18.

ROEDER, K. D., 1937. The control of tonus and locomotor activity in the praying mantis (*Mantis religiosa* L.). *J. Exp. Zool.*, **76**: 353–374.

ROEDER, K. D., 1953. Reflex activity and ganglion function. *In*: Roeder, K. D., Insect Physiology. New York, Wiley. Pp. 463–487.

ROEDER, K. D., L. TOZIAN AND E. A. WEIANT, 1960. Endogenous nerve activity and behaviour in the mantis and cockroach. *J. Ins. Physiol.*, **4**: 45–62.

ROWE, E. C., 1960. Activity of single nerve cells in an insect thoracic ganglion. *Anat. Rec.*, **137**: 389.

TEN CATE, J., 1941. Quelques remarques à propos de l'innervation des mouvements locomotoires de la Blatte (*Periplaneta americana* L.). *Arch. Néerl. Physiol.*, **25**: 401–409.

WEIS-FOGH, T., 1956. Biology and physics of locust flight. IV. Notes on sensory mechanisms in locust flight. *Phil. Trans. Roy. Soc., Ser. B*, **239**: 553–585.